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Systematics of the Calamarina Group of the Colubrid Snake Genus Tantilla

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Abstract. – Analysis of characteristics of color pattern and scutellation support the recognition of a calamarina species group of Tantilla consisting of four species: T. calamarina, T. cascadae, n. sp., T. coronadoi, and T. deppei. Tantilla martindelcampoi is synonymized with T. calamarina. Inter- and intragroup relationships are discussed.

The taxonomy of the colubrid snake genus Tantilla is now entering a synthetic stage, leaving behind a long period in which numerous discriminatory (sensu stricto) works were published. Over half of the 45 species currently considered valid were named before the beginning of the present century, most of them by Bocourt, Cope, and Günther. Since Boulenger's summary (1896) an additional 13 valid species were named (until 1950). Smith's (1942) important paper on Mexican Tantilla made the first serious attempt to assess relationships among the species of Tantilla then known to inhabit the United States and México. Most of the relationships he recognized have stood the test of time and this paper remains, in our opinion, the single most important work on the genus. Between 1950 and the present, eleven species were described. Since 1961, however, a number of nominal species have been relegated to synonymy or to subspecific status. Of 28 named species, 15 are now regarded as strict synonyms of valid species and the remainder are considered subspecies. Several recent papers dealt with the taxonomy of major sections of the genus (Smith, 1962; Tanner, 1966; Telford, 1966; McDiarmid, 1968; Wilson and Meyer, 1971; Wilson and Mena, 1980).

The present paper grew out of a study of some fifteen species of *Tantilla* occurring from Sinaloa to Argentina. Initially we were interested in the status of *T. armillata*, a name that had been applied to material from Honduras, El Salvador, Nicaragua, Costa Rica, and Panamá. The study encompassed members of the *melanocephala* group (sensu stricto), to which *armillata* purportedly belonged, but soon mushroomed to include all species of *Tantilla* with a dark middorsal stripe. Soon it was apparent that four closely related species (the *calamarina* group) could be separated from the Central and South American *melanocephala* group (Wilson and Mena, 1980). A new species in this group that has long been masquerading under the epithet *calamarina* is described below.

Justification For Recognition of the Calamarina Group

The four nominal species we consider to comprise the calamarina group are T. calamarina Cope, 1866, T. deppei (Bocourt), 1883, T. martindelcampoi Taylor, 1937, and T. coronadoi Hartweg, 1944. We furthermore consider T. martindelcampoi a junior synonym of T. calamarina; the documentation of that opinion is presented below.

In the description of Tantilla coronadoi Hartweg (1944) compared it to T. calamarina, T. martindelcampoi, and T. deppei (as well as to T. mexicana, a synonym of T. melanocephala – see Wilson and Mena, 1980) and stated that "although the resemblances of this form to calamarina and martindelcampoi are noteworthy, they appear superficial; the relationships between mexicana, deppei, and coronadoi are very probably closer genetically." Smith (1942) associated calamarina with martindelcampoi in the same division and deppei in another (apparently closer to the division containing mexicana).

The major factor that led us to recognize the calamarina group, within the genus Tantilla, including a new species described herein, is their similarity in head pattern. Head pattern is an important characteristic for assessing relationships within Tantilla (Smith, 1942) and the head pattern of these species appears distinct. All species also have a middorsal dark stripe. Tantilla calamarina, T. martindelcampoi, T. coronadoi, and the new species all have the central portion of the parietals covered with a spatulate anterior extension of the middorsal dark stripe, which continues anteriorly to cover the remainder of the head. On either side of this central head mark is a postparietal pale spot that usually grades posteriorly into the ground color of the dorsolateral field (area between the lateral and median dark stripes) and, in its bestdeveloped state, connects anteriorly with a narrow extension that proceeds along the side of the parietal, over the supraocular and onto the side of the prefrontals and internasals. Tantilla deppei has this same narrow pale marking around the rim of the dorsum of the head but it may or may not connect to a middorsally divided pale collar (the fact that pale nuchal marking appears more like a broken collar than a pair of nuchal or

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postparietal spots is due, perhaps, to the narrowness of the connection between the middorsal stripe and the dark pigment of top of the head).

The supralabials of all these forms are generally pale in color, with some dark pigment along their upper borders. In this manner they differ also from the members of the *Tantilla melanocephala* group, most of which also have a middorsal dark stripe, because the species comprising the latter group have a pre- and postorbital pale spot more or less separated by a subocular dark blotch (Wilson and Mena, 1980).

The species in the *calamarina* group basically have a middorsal dark stripe of variable width and a dark lateral stripe on rows 3 and 4 (except in *T. deppei*, in which there are sometimes two stripes, one on rows 2 and 3 and another on row 5, and in the new species, in which the lateral stripe on rows 3 and 4 disappears on the forepart of the body).

Tantilla calamarina Cope: Variation and the Status of T. martindelcampoi Taylor and Geophis gertschi Bogert and Porter

The close relationship between *Tantilla calamarina* Cope, 1866 and *T. martindelcampoi* has been recognized since Taylor described the latter species on the basis of a single specimen from south-central Guerrero and compared it to *Tantilla depressa* (=*Geagras redimitus* fide Smith, 1942) and *T. calamarina* (the questionable type locality of which is Guadalajara, Jalisco).

Although it is uncertain as to how many specimens of T. calamarina Taylor (1937) examined, the number of specimens available at that time was small (Smith, 1942). Apparently, the same sample size and the limited variation it showed plus a partially erroneous description of the color pattern of the holotype of T. martindelcampoi accounts for the description of the latter as distinct. We examined 39 specimens identified as T. calamarina and 2 identified as T. martindelcampoi (including the holotype) and conclude that the two are conspecific.

Taylor (1937) indicated that T. martindelcampoi differed from T. calamarina in lacking a preocular (present in calamarina), in having the fifth supralabial separated from the parietals (in contact in calamarina), and in having a lower number of ventrals and a higher number of subcaudals (114 and 39 compared to unstated ranges in calamarina). Although not mentioned by Taylor, Smith (1942) mentioned that they also differ in having the lateral dark stripe on rows 4 and 5 in martindelcampoi and 3 and 4 in calamarina.

Bogert and Porter (1966) described a new species, *Geophis gertschi*, from Colima. They assigned it to the genus *Geophis*, instead of *Tantilla*, because they thought the snake has a single anal plate. The single specimen upon which this nominal species is based is in poor condition but actually has a divided anal plate (Downs, 1967). Downs stated that "the divided anal, undivided sulcus, and absence of a loreal clearly exclude gertschi from the genus Geophis. These same features, together with extensive agreement in other characteristics of scutellation, coloration, body proportions, and hemipenial structure indicate that gertschi is a synonym of, or closely related to, Tantilla calamarina Cope."

We have examined the holotype of *Geophis gertschi* (AMNH 94877) and find it to be a typical Colima specimen of *Tantilla calamarina*. We herein relegate the name *Geophis gertschi* Bogert and Porter to the synonymy of *Tantilla calamarina* Cope.

In order to discuss variation and to assess the value of the characteristics formerly used to distinguish T. calamarina from T. martindelcampoi, we divided the total sample into six subsamples (termed populations A through F) from geographically restricted areas (Fig. 1).

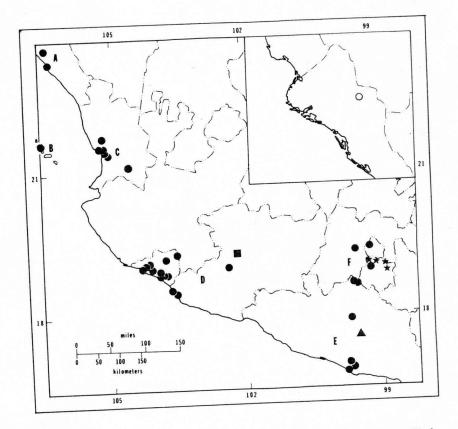


Fig. 1. Distribution of the four members of the *Tantilla calamarina* group. Circles represent localities for T. calamarina, squares for T. cascadae, triangles for T. coronadoi, and stars for T. deppei. Inset is of northern Sinaloa showing literature record for T. calamarina reported by McDiarmid, Copp, and Breedlove (1976).

Analysis of Variation

All specimens possess the following characteristics: dorsal scale rows 15 throughout; first pair of infralabials separated by contact of mental and anterior chinshields; postoculars 1-1; temporals 1+1; anal plate divided. Most specimens have 6-6 supralabials (two specimens from Guerrero have 6-5 and 5-5 supralabials), 6-6 infralabials (two specimens, one from Sinaloa and one from Colima, have 5 infralabials on one side and 6 on the other).

Condition of the Preocular. – Taylor (1937) implied that a given specimen either has (calamarina) or lacks a preocular scale (martindelcampoi). Our data (Table 1) indicate that all specimens known from populations A-C have a preocular, whereas 25.9% of those from populations D-F lack a preocular on one or both sides. Thus in no population is a lack of a preocular scale exclusively the case (the holotype of *T. martindelcampoi* belongs to population E). In addition, even in those specimens with a preocular, there is a decrease in its size proceeding southward, as indicated by an increasing lack of contact between the preocular and the postnasal scales (Table 1); this is a much easier fashion to judge the size of the preocular than by measuring it.

Supralabial-Parietal Contact. - Taylor (1937) also implied that the fifth supralabial either is in contact with the parietal (*calamarina*) or is not (*martindelcampoi*). Our data (Table 2) demonstrate that all conditions between a broad contact and a broad separation of the supralabial and parietal exist without a discernible geographic pattern.

Ventrals. - The male holotype of Tantilla martindelcampoi has 114 ventrals and Taylor (1937) considered this distinctively lower than counts for T. calamarina, although he gave no counts for the latter. The only specimen of T. calamarina mentioned by Taylor in that paper is a female from Colima with a ventral count of 131. Male Tantilla characteristically have fewer ventrals than do females so such a difference in ventral count is not unexpected. Our data on ventral counts (Table 3) suggest a clinal decrease in ventral number proceeding southward but the nature of the cline is unclear.

The specimen from the Tres Marías Islands has a count comparable to specimens from 350 kilometers to the southeast on the mainland (Colima). McDiarmid, Copp, and Breedlove (1976) pointed out that *Tantilla calamarina* and *T. bocourti*, the two species of *Tantilla* on the Tres Marías Islands, are exceptions to the general rule that snakes on these islands average more ventrals than their mainland counterparts.

In addition, specimens from the higher elevations of Guerrero, México, Morelos, and the Distrito Federal (population F) have higher mean ventral counts than those from central Guerrero (population E) and Colima and Michoacán (population D). Subcaudals. - Taylor (1937) considered the subcaudal count (39) of the male holotype of *Tantilla martindelcampoi* to be significantly higher than counts for *calamarina*. The Colima female *T. calamarina* discussed in the same paper has 29 subcaudals. Male *Tantilla* characteristically have more subcaudals than do females as substantiated by our data (Table 3).

Color pattern. - Smith (1942) mentioned that Tantilla martindelcampoi can be distinguished from T. calamarina by the presence of the lateral stripe on the adjacent halves of rows 4 and 5, instead of rows 3 and 4. This distinction was echoed by Hartweg (1944) and Smith and Taylor (1945). Peters (1954) pointed out that the specimen of T. calamarina from Queseria, Colima was stated by Taylor (1937) to have the lateral dark stripe on rows 4 and 5, as also was stated to be the case in the holotype of T. martindelcampoi, described in the same paper. We suspect that Taylor (1937) did not make the distinction between the two species in lateral stripe placement because none existed. The distinction was made subsequently (Smith, 1942). We have seen no specimens assigned to either calamarina or martindelcampoi with a lateral dark stripe placed elsewhere than on rows 3 and 4, including the holotype of martindelcampoi and the Colima calamarina discussed in Taylor's 1937 paper.

There are geographic differences in pattern, some of which were alluded to by Zweifel (1960) and McDiarmid, Copp, and Breedlove (1976). These differences involve the width and definition of the middorsal dark stripe and, to a lesser extent, the definition of the lateral stripe. In all but one specimen (AMNH 19750) from populations A, B, and C, the middorsal stripe is confined to the middle of the middorsal row (Fig. 2A). In all members of populations D, E, and F, the middorsal dark stripe covers all of row 8 and in all but one specimen, the adjacent portions of rows 7 and 9 (Fig. 2B).

In all specimens in populations A, B, and C the lateral stripe is found on the upper edge of row 3 and lower edge of row 4 or on the middle of row 3 and the middle of row 4 (Fig. 2A). In at least 20 of 30 specimens from populations D, E, and F the lateral stripe is broader and better-defined, being present on the upper half of row 3 and the lower half of row 4 (Fig. 2B). In the remainder of the specimens the stripe is either too faded to determine its precise nature or is as narrow as it is in some of the more northern specimens.

There is some variation in the head pattern but it does not appear to be geographic. In some specimens the postparietal pale spots are relatively large and prominent and in others they are smaller. The anterior extensions of the pale nape markings are well-defined and complete (at least to behind the eye) or they are broken and poorly-defined. In some specimens this anterior extension is absent.

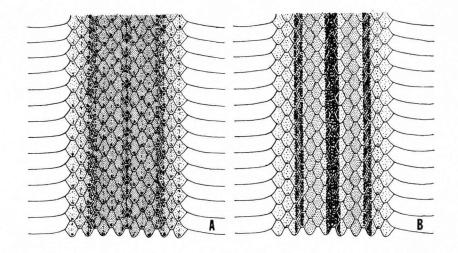


Fig. 2. Dorsal color patterns of two specimens of *Tantilla calamarina* showing the range of variation in width of middorsal and lateral stripes. A. UF/FSM 24788, 16.3 mi NW Tepic, Nayarit, México. B. UMMZ 125723, 23 mi SE Manzanillo, Colima, México.

Taxonomic Assessment

Analysis of variation in five characters or character complexes that have been used in the past as justification for the distinction between two nominal species, Tantilla calamarina and T. martindelcampoi, shows that: (1) the number of specimens lacking a preocular or showing a decrease in the size of the preocular (as gauged by the presence or absence of contact between the postnasal and preocular) increases proceeding southward through the range; (2) there is a gradation between a condition where the fifth supralabial and parietal are widely separated to one in which they are broadly in contact without a discernible geographic trend or pattern; (3) there is a gradual clinal decrease in ventral number toward the southern portion of the range; (4) all specimens (including the holotype of T. martindelcampoi) have the dark lateral line positioned on rows 3 and 4 but specimens from Sinaloa, Nayarit, and the Tres Marias Islands have a narrower middorsal stripe and narrower and poorly-defined lateral stripe, as compared to most specimens from portions of the range to the south.

It is obvious that the characters used by Taylor (1937) to distinguish between *T. calamarina* and *T. martindelcampoi* do not in fact do so and that no additional means of distinguishing them has emerged from this study. It is our opinion, therefore, that the name *Tantilla martindelcampoi* Taylor, 1937 should be relegated to the synonymy of *Tantilla calamarina* Cope, 1866.

		Pre	oculars		Preocular-Postnasal Contact			
Population	Ν	0-0	0-1	1-1		Yes	Yes/No	No
A	2	_	_	2	2	2	-	-
В	1	_	-	1	1	1	-	-
C	6	_	_	6	6	4	_	2
D	19	1	1	17	17	7	1	9
E	4	3	_	1	1	-		1
F	7	2	-	5	5	1	-	4

Table 1. Variation in the condition of the preocular in populations from the combined ranges of *Tantilla calamarina* and *T. martindelcampoi*. Location of the populations is indicated in Figure. 1.

Table 2. Variation in the degree of contact or lack of contact between the fifth supralabial and parietal in populations from the combined ranges of *Tantilla calamarina* and *T. martindelcampoi*. Location of the populations is indicated in Figure 1. Counts for both sides of the head are included.

Population	N	Separated	Barely Separated	Barely in Contact	In Contact
A	2	1	1	1	1
В	1	1	1	-	-
C -	6	11	1	-	-
D	18	9	11	5	10
Е	4	8	-	-	-
F	7	6	2	-	6

Table 3. Variation in the number of ventrals and subcaudals in populations from the combined ranges of *Tantilla calamarina* and *T. martindelcampoi* (auctorum). Location of the population is indicated in Figure 1. Population statistics are arranged as follows: range (mean) sample size.

4.

	Ven	trals	Subcaudals		
Population	Males	Females	Males	Females	
A	126		35	-	
В	115	-	30	-	
С	133	123-140(133.0)5	33	25-29(26.4)5	
D	114-122(118.8)7	123-132(128.2)12	31-42(40.4)7	26-33(30.1)11	
Е	113-122(116.3)3	123	37-39(37.6)3	29	
F	121-124(122.3)3	126-137(130.2)4	34-39(36.3)3	25-28(27.0)4	
Total	113-133(120.3)16	123-140(129.4)22	30-42(36.6)16	25-33(28.6)2	

Species Accounts

Tantilla calamarina Cope

- Tantilla calamarina Cope, 1866: 320, 1876: 143, 1887: 84; Bocourt, 1883: 581; Dunn, 1928: 3; Amaral, 1930: 220; Oliver, 1937: 24; Taylor, 1937: 346, 1939: 483; Taylor and Smith, 1938: 254; Smith, 1940: 60, 1942: 35, 1943: 474; Hartweg, 1944: 4; Smith and Taylor, 1945: 137; Schmidt and Shannon, 1947: 83; Duellman, 1954: 21, 1958: 17, 1961: 110, 1965: 655; Peters, 1954: 30; Zweifel, 1959: 3, 1960: 110; Cochran, 1961: 216; Hardy and McDiarmid, 1969: 202; Clark, 1970: 130; McDiarmid, Copp, and Breedlove, 1976: 12.
- Tantilla bimaculata Cope, 1876: 143 (Holotype, USNM 6834; typelocality: Mazatlán, Sinaloa, México); Cope, 1887: 84; Cochran, 1961: 216.
- Homalocranion bimaculatum: Bocourt, 1883: 580.

Homalocranium bimaculatum: Günther, 1895: 154.

Homalocranium calamarinum: Boulenger, 1896: 227.

- Tantilla martindelcampoi Taylor, 1937: 347 (Holotype, UIMNH 25062; type-locality: near El Treinta, 1 mi N Organos, Guerrero, México), 1939: 483; Smith, 1940: 60, 1942: 37; Hartweg, 1944: 4; Smith and Taylor, 1945: 139; Peters, 1954: 31; Duellman, 1965: 680. New synonymy.
- Geophis gertschi Bogert and Porter, 1966: 1 (Holotype, AMNH 94877; type-locality: 2 mi S Tonila, Jalisco, in Colima, México); Downs, 1967:

113. New synonymy.

Holotype. - USNM 6600.

Type-locality. - Guadalajara, Jalisco, México. Locality questioned by Peters, 1954: 31, and Zweifel, 1959: 6.

Definition. - A member of the Tantilla calamarina group with usually 6 supralabials, 113 to 133 ventrals in males and 123 to 140 in females, 30 to 42 subcaudals in males and 25 to 33 in females, one postocular, 1+1temporals, dark middorsal stripe occupying as little as the middle of the middorsal row or as much as the middorsal row and adjacent halves of rows 7 and 9, dark lateral stripe on rows 3 and 4 (frequently on adjacent halves of those rows), and head pattern consisting of a spatulate dark anterior extension of the middorsal dark stripe flanked by two pale postparietal spots (Figs. 2, 3).

Description. - Tantilla calamarina is tan to brown dorsally grading to cream ventrolaterally. The brown to dark brown middorsal stripe occupies from as little as the middle of the middorsal row to as much as all of the middorsal row and the adjacent halves of rows 7 and 9. The brown to dark brown lateral stripe occupies as little as the adjacent edges of rows 3 and 4 or the middle of each of rows 3 and 4 to as much as the adjacent halves of rows 3 and 4.

A spatulate extension of the dark middorsal stripe occupies most of the upper surface of the head and is flanked on either side by a pale narrow anterior extension of the dorsolateral field, which in its bestWILSON/MEYER: CALAMARINA GROUP OF TANTILLA

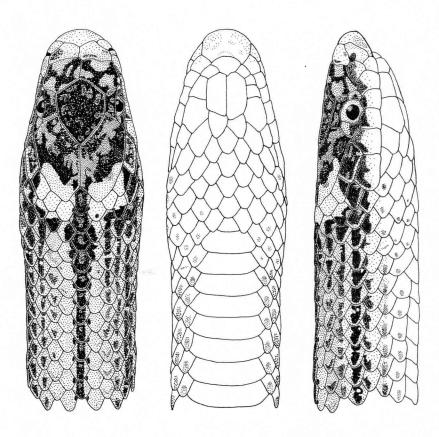


Fig. 3. Dorsal, ventral, and lateral views of head of *Tantilla calamarina* (AMNH 78745, María Madre Island, Tres Marías Islands, Nayarit, México).

developed form passes along the lateral edge of the parietals, supraoculars, prefrontals, and internasals to join its partner on the upper portion of the rostral. The lateral dark stripe continues anteriorly along the side of the head across the temporals, lower portion of the postocular, around the eye and onto the preocular and postnasal. The lower edge of this "mask" passes along the upper edge of the supralabials, which are otherwise cream-colored. The venter is immaculate cream.

Variation in scutellation may be summarized as follows: preocular present on both sides (80.5% of specimens examined), on only one side (2.9%), or absent (16.6%); if preocular is present, it may be in contact with postnasal on both sides of head (50.0%), only on one side (3.3%), or

neither side (46.7%); fifth supralabial separated from parietal (47.2% of both sides of heads of specimens examined), barely separated (22.2%), barely in contact (6.9%), or in marked contact (23.7%); first pair of infralabials invariably separated from one another; ventrals in males 113-133 (\bar{x} =120.3), in females 123-140 (129.4); subcaudals in males 30-42 (36.6), in females 25-33 (28.6).

Total lengths of 16 male snakes range from 72-91 mm, of 22 females, 104-202 mm, and tail length ranges from 13-36 in males, in females 13-29 mm. Relative tail length in males ranges from 15.8-21.1%, in females, 11.0-15.5%.

Range. - Low, moderate, and intermediate elevations (sea level to approximately 1653 meters) of the Pacific versant of México from Sinaloa to Guerrero and Morelos, including the Tres Marías Islands (Fig. 1). Smith (1942) listed a record from Tezuitlán, Puebla. We have not seen the specimen upon which this record is based.

Ecological Distribution. - These snakes occur in habitats ranging from arid thorn scrub to moist pine woodland in Tropical Arid Forest, Tropical Dry Forest, Subtropical Dry Forest, Subtropical Moist Forest, and Lower Montane Moist Forest formations (Holdridge, 1964). These vegetational formations in various areas have been described by Duellman (1958, 1965), Goldman (1951), and Hardy and McDiarmid (1969).

Specimens Examined. - MÉXICO. SINALOA: Cañon Tarahumares at Vado Ceboletas (JFC 69-91 - not examined); Mazatlán (USNM 6834 holotype of T. bimaculata); 18 mi N Mazatlán (MCZ 61430). NAYARIT: 7.1 mi N Compostela, 3200' (UF/FSM 24789); nr. El Ocotillo (AMNH 19743); San Blas (BMNH 81.10.1.11); 7.5 mi E San Blas (CAS 95770); between Santa Cruz and Tepic (CAS 104979); 16.3 mi NW Tepic, 450' (UF/FSM 24788); Tres Marías Islands, María Madre Id. (AMNH 78745). COLIMA: 4 mi N Colima (AMNH 12775); Ejido de Tepextle, 4 mi ENE Manzanillo (UMMZ 115587); Manzanillo (CAS 121076); 12 mi E Manzanillo (AMNH 91593); 13 mi (by Hwy. 80) SE Manzanillo (UMMZ 125722); 11.7 mi NE Manzanillo on Hwy. 110 (UF/FSM 29872); 25 mi S Manzanillo (UIMNH 53056); 23 mi (by rd.) SE Manzanillo (UMMZ 125723); Paso del Río (UMMZ 110872); Queseria (UMMZ 80223-25); nr. Queseria (UIMNH 18787-88); 2.7 mi ENE Tecolapa, 800' (UF/FSM 24758); Tecomán (AMNH 12776); 5 mi E Tecomán (AMNH 19746); 2 mi S Tonila, Jalisco (AMNH 94877 holotype of Geophis gertschi). JALISCO: Guadalajara (USNM 6600 - not mapped). MICHOACAN: Apatzingan (Schmidt and Shannon, 1947 - not examined); 0.5 mi SW La Placita (UMMZ 104499); 3 mi S San Juan de Lima (UMMZ 11446-47). GUERRERO: Acapulco (SDSNH 46306); summit, 4 mi W Cacahuamilpa (AMNH 99141); El Limoncito (UIMNH 25062); 8 mi N Taxco, 5500' (TCWC 7433); nr. El Treinta, 1 mi N Organos (UIMNH 25062 - holotype of T. martindelcampoi); 3.8 mi SW Xochipala, 4500' (UF/FSM 29871). MORELOS: Progreso (UIMNH 24696-97); Cuernavaca (USNM 110386). DISTRITO FEDERAL: S of Santa Fe (AMNH 19750). MÉXICO: valley of México and Toluca (USNM 32290).

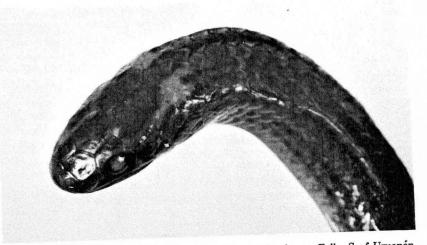


Fig. 4. Head of Tantilla cascadae (AMNH 107389, Tzaráracua Falls, S of Uruapán, Michoacán, México).

Tantilla cascadae, new species

Holotype. - AMNH 107389, female.

Type-locality. - Tzaráracua Falls [=Cascada la Tzaráracua], S of Uruapán [10.5 km south, according to Duellman, 1961], Michoacán, México, collected in June, 1939, by D. F. Brand.

Definition. - A member of the Tantilla calamarina group with 6 supralabials, 139 ventrals, 37 subcaudals, two postoculars, 1+1 temporals, dark middorsal stripe occupying middle of middorsal scale row, dark lateral stripe absent except on neck region where it occupies adjacent edges of rows 3 and 4, and head pattern consisting of a spatulate dark anterior extension of the middorsal dark stripe flanked by a pale narrow longitudinal markings connected to pale postparietal spots (Figs. 4, 5A).

Description of the Holotype. - A female with 15 dorsal scale rows, smooth throughout, 139 ventrals, divided anal plate, 37 subcaudals, measurements not determinable because of desiccated condition of the holotype.

Nasal scale completely divided, the posterior section in contact with single preocular on both sides of head; two postoculars, lower one smaller; one anterior and one posterior temporal, both elongate; supralabials 6-6, with 3rd and 4th entering orbit, last one largest; infralabials 5-6, three in contact with anterior chinshields on left (3rd largest) and four on right (4th largest), first pair separated medially by contact of mental and anterior chinshields; anterior chinshields longer than posterior pair.

Dorsal ground color pale brown. Dark brown middorsal stripe consisting of a series of more or less disjunct elongate spots on the middle of the middorsal row. This stripe expands anteriorly to cover the middorsal row and adjacent halves of the paravertebral rows at a point about 3 scales posterior to the parietals and continues posteriorly to the end of the tail. The lateral stripe is apparent only on the neck region (to a point approximately opposite the 17th ventral) where it occupies the adjacent edges of rows 3 and 4. The venter is cream except for a slight amount of brown pigment on the posterolateral edge of each ventral.

The head pattern consists of a spatulate extension of the middorsal stripe flanked by two ivory-colored postparietal spots from which emanate narrow anterior extensions which pass along the side of the parietals, across the supraoculars, prefrontals, and internasals, and onto the dorsal portion of the rostral. The spatulate head figure is mottled with ivory, giving the dorsum of the head a lichenous appearance. The postparietal spots do not grade into the ground color of the dorsum of the body. The short lateral stripe broadens and continues anteriorly across the parietals and upper portion of the supralabials, around the eye, and onto the preocular and postnasal. The remainder of the supralabials are cream. The chin is cream-colored.

Comparisons. - Tantilla cascadae differs from *T. calamarina* in having two postoculars instead of one and no dark lateral stripe beyond the neck region, instead of a well-developed one extending the length of the body. *Tantilla cascadae* has six supralabials, 139 ventrals in the single known specimen, the anterior and posterior temporal scales in mutual contact, and no dark lateral stripe beyond the neck region; *T. coronadoi* has seven supralabials, 158 and 165 in two known specimens, the anterior and posterior temporal scales separated by contact of the seventh supralabial and parietal, and a well-developed dark lateral stripe extending the length of the body. *Tantilla cascadae* possesses six supralabials, 139 ventrals and 37 subcaudals in the single known female specimen, no dark lateral stripe beyond the neck region, and no pale nuchal collar; *T. deppei* has seven supralabials, 153-168 ventrals and 43-48 subcaudals in females, a well-developed dark lateral stripe extending the length of the longed dark lateral stripe extending the length of the body, and a pale nuchal collar.

Range. - Known only from the type locality (Fig. 1).

Ecological Distribution. - Known only from the Lower Montane Moist Forest formation (Holdridge, 1964). The holotype and only known specimen of *Tantilla cascadae* was collected in the vicinity of Tzaráracua Falls on the slopes of the Sierra de los Tarascos in Michoacán at an approximate elevation of 1430 m (elevation according to Duellman, 1961: 140). This is an area covered by oak forest with a few scattered pines (Duellman, 1961). Duellman (1965, pl. 35, fig. 2) provided a photograph of the area.

Tantilla coronadoi Hartweg

Tantilla coronadoi Hartweg, 1944: 4; Smith and Taylor, 1945: 137; Davis and Dixon, 1959: 87; Duellman, 1965: 683, 685.

Holotype. - UMMZ 85697, female.

Type-locality. - vicinity of Chilpancingo, Guerrero, México.

Definition. - A member of the Tantilla calamarina group with 7 supralabials, ventrals 158 in only known male and 165 in only known female, subcaudals 35+(?) in male and 40 in female, usually 2 postoculars, anterior temporal separated from posterior one by contact of seventh supralabial and parietal, middorsal dark stripe occupying middle of middorsal row, lateral dark stripe occupying row 3 and adjacent one-half to all of scale row 4, and head pattern consisting of a spatulate dark anterior extension of middorsal dark stripe flanked by two pale anterior extensions of dorsolateral field (Figs. 5B, 6).

Description. - Tantilla coronadoi has a tan to pale brown dorsal ground color. The dark brown middorsal stripe is confined to the median third of the middorsal row, except for the first 5 to 7 scales posterior to the parietals where it involves all of the middorsal row and the adjacent halves of the paravertebral rows. The lateral stripe is brown to dark brown and is poorly- to well-defined but appears to occupy all of row 3 and at least half, if not all, of row 4. There are also diffuse, narrow dark lines on rows 5, 6, and 7.

The head pattern is essentially like that of T. calamarina, consisting of a spatulate extension of the middorsal dark stripe that covers much of the upper surface of the head. On either side of this figure is a narrow pale anterior extension of the dorsolateral field that passes along the outer portion of the parietals, across the supraoculars and onto the prefrontals and internasals to join with its partner on the upper portion of the rostral. The lateral dark stripe which fuses with a dark stripe on row 5 just behind the head continues anteriorly across the temporals and upper portions of the supralabials, around the eye, and onto the preocular and postnasals. The remainder of the supralabials are creamcolored. The venter is immaculate cream.

Variation is scutellation may be summarized as follows: preocular present and in contact with postnasal; fifth supralabial separated from parietal; infralabials 6; first pair of infralabials in contact medially or not; ventrals 158 in one male, 165 in one female; subcaudals 35+(?) in male, 40 in female.

Total length 171 mm and tail length 28 mm in male; 183 and 31 in female. Relative tail length in male 0.164, in female 0.169.

Range. - Moderate and intermediate elevations (1402 to 1524 meters) of the Pacific versant in central Guerrero (Fig. 1).

100.7

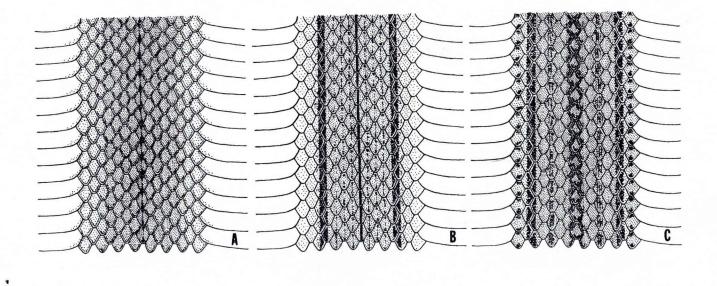


Fig. 5. Dorsal color patterns of three of the members of the *Tantilla calamarina* group: (A) *T. cascadae* (AMNH 107389); (B) *T. coronadoi* (TCWC 9528); (C) *T. deppei* (AMNH 94719, ca. 15 mi NNE Cuautla, nr. Totolapan, Morelos, México).

WILSON/MEYER CALAMARINA GROUP OF TANTILLA

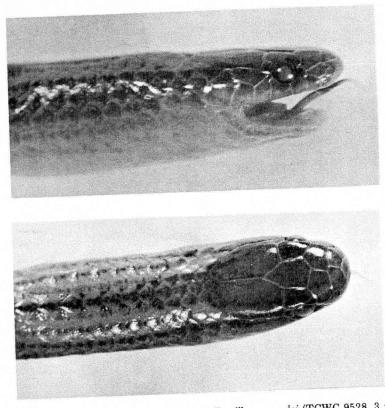


Fig. 6. Lateral and dorsal views of head of Tantilla coronadoi (TCWC 9528, 3 mi W Chilpancingo, Guerrero, México).

Ecological Distribution. - Occurs in the Subtropical Dry Forest formation (Holdridge, 1964). This area has been further characterized by Goldman (1951) and Davis and Dixon (1959) cited a specimen as having been collected in an area covered by "chaparral and grasses." Specimens Examined. - MÉXICO. GUERRERO: vicinity of Chil-

pancingo (UMMZ 85697 - holotype); 3 mi W Chilpancingo, 5000' (TCWC 9528).

Tantilla deppei (Bocourt)

Homalocranion deppei Bocourt, 1883: 584.

Tantilla deppei: Cope, 1887: 83; Smith, 1942: 36; Hartweg, 1944: 4; Smith and Taylor, 1945: 138; Davis and Smith, 1953: 137; Duellman, 1965: 683; Clark, 1970: 130.

Homalocranium deppei: Günther, 1895: 151.

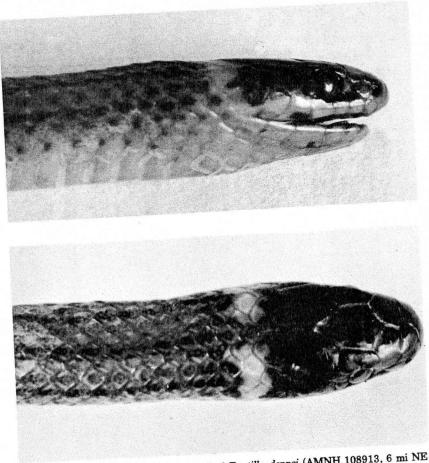


Fig. 7. Lateral and dorsal views of head of Tantilla deppei (AMNH 108913, 6 mi NE Tepoztlán, Morelos, México).

Homalocranium miniatum: Boulenger, 1896: 222 (nec Cope). Lectoholotype. - MNHN 54, adult male; whereabouts of other specimens in the Paris and Berlin museum unknown (H. M. Smith, pers.

Type-locality. - "Mexico." M. Ghiesbreght, collector. Restricted to comm.). vicinity of Huitzilac, Morelos, México by Davis and Smith, 1953: 138.

Definition. - A member of the Tantilla calamarina group with usually 7 supralabials, 142 to 150 ventrals in males and 153 to 168 in females, 54to 60 subcaudals in males and 43 to 48 in females, 2 postoculars, 1+1temporals, middorsal dark stripe occupying as little as all of middorsal scale row to as much as the middorsal row and adjacent halves of rows 7 and 9, dark lateral stripe on row 3 or rows 2 and 3, and head pattern

consisting of spatulate dark anterior extension of middorsal dark stripe flanked by narrow longitudinal pale marking and short pale middorsally interrupted nuchal collar (Figs. 5 C, 7).

Description. - Tantilla deppei has a tan to brown ground color. The middorsal stripe is brown to dark brown, diffuse, and occupies from as little as all of the middorsal row to as much as the middorsal row and adjacent halves of rows 7 and 9. The lateral stripe is also generally diffuse, brown in color, and occupies as little as most of row 3 or as much as the adjacent halves of rows 2 and 3. There is also a dark stripe on row 5 which is usually more poorly-defined than the lateral stripe, and one sometimes on row 1, although there is more often a series of dark dots.

The head pattern consists of a spatulate extension of the dark middorsal stripe that occupies most of the upper surface of the head. This figure is flanked on either side by pale narrow markings that begin on the parietals and extend anteriorly across the supraoculars, prefrontals, and internasals to meet on the dorsal portion of the rostral. Below this marking is a dark band that begins on the posterior temporal and passes anteriorly across the anterior temporal and upper edges of the supralabials, and onto the preocular and nasal scale. The remainder of the supralabials are cream. The head cap is bounded posteriorly by a short pale nuchal collar, which is broken middorsally by the middorsal dark stripe and set off markedly from the ground color of the dorsolateral field. The venter is immaculate cream.

Variation in scutellation may be summarized as follows: preocular present and in contact with postnasal; supralabials usually 7-7 (94.4%), but sometimes 6-6 (5.6%); fifth supralabial separated from parietal; first pair of infralabials usually separated by contact of mental and anterior chin shields (88.8%), but sometimes in contact medially (11.2%); ventrals in males 142-150 ($\bar{x}=145.7$), in females 153-168 (159.9); subcaudals in males 54-60 (56.9), in females 43-48 (45.8).

Total length in male snakes ranges from 98-268 mm, in females, 95-268 mm, and tail length in males ranges from 22-62 mm, in females, 16-49 mm. Relative tail length in males ranges from 22.4-25.4%, in females 16.6-18.8%.

Range. - Intermediate elevations (1524 to 2438 meters) of northern Morelos, México (Fig. 1).

Ecological Distribution. - Occurs in the Lower Montane Moist Forest formation (Holdridge, 1964). Davis and Smith (1953) reported finding specimens "under rocks in open pine-oak association."

Specimens Examined. - MÉXICO. "Southern México" (BMNH 90.4.24.34). MORELOS: No other data, restricted to vicinity of Huitzilac (MNHN 54); 6 mi NW Coajomulco (INHS 8232); ca. 15 mi NNE Cuautla, nr. Totolapan (AMNH 94718-19); 20 km NE Cuautla, 6500' (TCWC 7347-48, 7354); Cuernavaca (LACM 64505); 1.5 mi SE Huitzilac, 8000' (TCWC 7346, 7349-53; UIMNH 25933-34); 6 mi NE Tepoztlan, 7000-8000' (AMNH 108913).

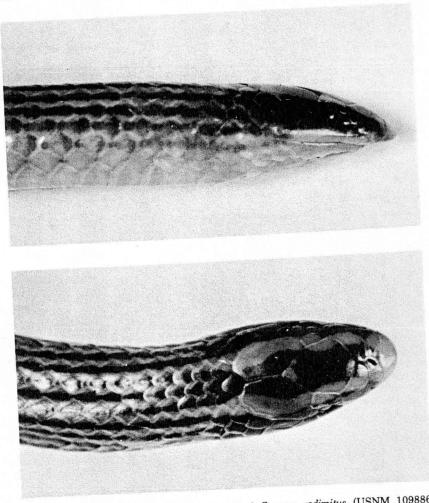


Fig. 8. Lateral and dorsal views of head of Geagras redimitus (USNM 109886, Tehuantepec, Oaxaca, México).

Relationships

Two pieces of information indicate that the monotypic genus Geagras might be related to the calamarina group of the genus Tantilla. First, Dunn (1928) described a new species, Tantilla depressa, from Oaxaca, which species was synonymized with *Geagras redimitus* by Smith (1942). Later, Smith (1943) stated that "this curious snake bears no relationship to Geophis, near which it is allocated by Boulenger. It more nearly resembles Tantilla, as concluded by Dunn."

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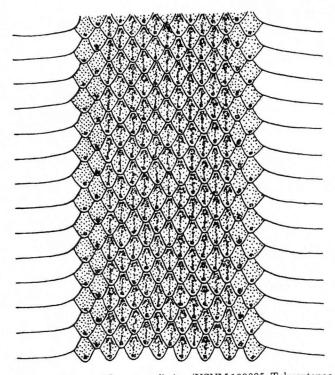


Fig. 9. Dorsal color pattern of *Geagras redimitus* (USNM 109885, Tehuantepec, Oaxaca, México).

We have examined a portion of the sample of G. redimitus from Oaxaca reported by Smith (1943) in order to assess its relationship to members of the T. calamarina group.³ Upon superficial examination, it became obvious that there is considerable resemblance between G. redimitus (Figs. 8, 9) and T. calamarina, but less so between redimitus and other members of the calamarina group. They share the following characteristics: tendency to lose the preocular; if the preocular is present, there is a tendency for it to be separated from the postnasal (always separated in *Geagras*); single postocular; tendency for separation of the postocular and anterior temporal by contact of parietal with supralabials; first pair of infralabials separated; low numbers of ventrals and subcaudals; dorsal head pattern of spatulate figure bounded by narrow pale markings.

Geagras redimitus differs from T. calamarina primarily in features that reflect the apparent greater specialization for fossorial living in Geagras. In Geagras the head is more pointed, the rostral is acute and produced,

³ Duellman (1961) incorrectly identified two specimens of *T. calamarina* (UMMZ 114446-47) from Michoacán as Geogras redimitus. the eye is relatively smaller, the prefrontals are relatively smaller, the supralabials number 5 (as opposed to 6 in *calamarina*), and only the 3rd supralabial enters the orbit (3+4 in *calamarina*). Smith and Taylor (1945) distinguished the genus *Geagras* from *Tantilla* in their key on the basis of six supralabials and 1+2 temporals in former as opposed to six or seven supralabials and 1+1 temporals in the latter. As pointed out above, *Geagras* has 5 supralabials, not six, and the temporals are 1+1, as in *Tantilla*.

The genus Tantilla, with the description of T. cascadae in this paper, contains 45 species. The genus includes small, slender snakes with the head not noticeably distinct from the body, 15 smooth dorsal scale rows throughout, divided anal plate, no loreal, paired subcaudals, and posterior grooved fangs on the maxilla (Hardy and Cole, 1968). Other characteristics show more variation. The preocular is single or absent (the latter condition is present in some specimens of T. calamarina). The postoculars are usually 2, but are characteristically 1 in some species (albiceps, calamarina, and gracilis). Infralabials number usually 6, but sometimes 7 (according to Smith, 1942). Supralabials usually number 7, but are 6 in some species (calamarina, cascadae, and gracilis). Ventrals in the entire genus number from 103 (in canula) to 197 (planiceps). Low ventral numbers (below about 140) occur in T. canula, vermiformis, schistosa, relicta, calamarina, and gracilis. Subcaudals in the entire genus range from 21 (brevicauda) to 82 (rubra). Low numbers are found in T. brevicauda, calamarina, vermiformis, schistosa, and striata. It appears that T. calamarina shows the greatest amount of divergence from the typical Tantilla condition. In other words, T. calamarina is the most atypical Tantilla in our opinion. It is, therefore, of interest to note its resemblance to Geagras redimitus. In four of the features in which calamarina departs from the norm in Tantilla (tendency toward absence of preocular, number of postoculars, low numbers of ventrals and subcaudals) it agrees with Geagras. In the other features (number of supralabials) Geagras shows a further reduction and specialization for a fossorial mode of life. All Tantilla have two supralabials entering the orbit, whereas Geagras has but one.

Upon consideration of the above information, it is our opinion that T. calamarina is closely related to Geagras redimitus. We feel, however, that inclusion of the latter species in the genus Tantilla would unduly broaden the generic definition. The relationships of T. calamarina, nevertheless, appear to us to be closer to the other members of the calamarina group than to Geagras and we do not wish to switch calamarina to the genus Geagras. It is of interest to note that T. calamarina appears to be the species of Tantilla most highly specialized for a fossorial existence and Geagras redimitus appears to be another step in a morphocline of increased fossorial adaptation. In addition to the departures made by T. calamarina, Geagras has a more attenuate head, smaller eye and lower number of supralabials.

With regard to intragroup relationships, it appears that there are probably three subgroups, one containing T. deppei, the least specialized member of the group, a second containing T. coronadoi, and a third containing T. calamarina and T. cascadae. Tantilla deppei probably will eventually be shown to have some degree of relationship with members of the melanocephala group. It differs principally from those snakes in lacking a dark nape band. Tantilla coronadoi seems to be more closely related to T. calamarina and T. cascadae than to T. deppei, judged on the basis of similarity of color patterns. Tantilla coronadoi is unique within the genus, however, in the possession of a contact between the seventh supralabial and the parietal. It also possesses 7 supralabials and a higher number of ventrals than either calamarina or cascadae. Tantilla calamarina is apparently less closely related to T. deppei and T. coronadoi than is \hat{T} . cascadae. Tantilla cascadae has a more "normally" shaped head for a Tantilla, two postoculars and a higher number of ventrals than does T. calamarina.

Key to the Species of the Tantilla calamarina Group

1. Seventh supralabial in contact with parietal, separating anterior temporal from posterior one coronadoi Seventh supralabial separated from parietal, anterior and posterior temporals in contact with one another
2. Pale nuchal collar present, divided medially; supralabials usually 7; ventrals more than 140
3. Two postoculars; dark lateral stripe present only on fore- bodycascadae Single postocular; dark lateral stripe extends length of bodycalamarina

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